

## Ecophysiological traits and activity patterns of coleopterans from Atacama Desert provide clues to the functional responses of small ectotherms to climate change

Carlos Tirado<sup>a</sup>, Daniel Trujillo<sup>a</sup>, Jaime Pizarro-Araya<sup>b,c</sup>, Fermín M. Alfaro<sup>b,c</sup>, Sylvana González<sup>d</sup>, Miguel A. Carretero<sup>e,\*</sup>

<sup>a</sup> Departamento de Química y Biología, Facultad de Ciencias Naturales, Universidad de Atacama, Casilla 576, Copiapó, Chile

<sup>b</sup> Laboratorio de Entomología Ecológica, Departamento de Biología, Facultad de Ciencias, Universidad La Serena, Casilla 554, La Serena, Chile

<sup>c</sup> Instituto de Investigación Multidisciplinaria en Ciencia y Tecnología, Universidad de La Serena, La Serena, Chile

<sup>d</sup> Centro de Educación y Capacitación de la Universidad Católica del Norte, Miraflores N°475, Coquimbo, Chile

<sup>e</sup> CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, N° 7. 4485-661 Vairão, Vila do Conde, Portugal



### ARTICLE INFO

#### Keywords:

Thermoregulation  
Water loss  
Activity  
Deserts  
Climate change  
Functional response

### ABSTRACT

There is an increasing contribution of ecophysiology in community ecology and climate change contexts. As such, functional patterns under extreme water and temperature restrictions in deserts can provide inference of the responses of small ectotherms to climate change. However disentangling the interactive effects between both factors requires experimental evidence. Here we took advantage of a *flowering desert* episode promoting a population bloom in *Gyriosomus* (Coleoptera: Tenebrionidae) beetles from Atacama Desert to test this interactive hypothesis. By systematically sampling two sympatric *Gyriosomus* species, we analyzed the differences in activity, body temperature and water loss rate. Body size regardless the species or sex was responsible for the observed behavioral and ecophysiological patterns. Large coleopterans (females > males, *G. kingi* > *G. planicollis*) lost less water and were active at higher temperatures making their bimodal diel activity less marked. Beyond the confirmation of the crucial role of water availability and inactivity in arid ecosystems, these results suggest that functional responses of small ectotherms to climate change will be size-dependent while advocate for integrating hydric and thermal data to better understand this transition.

### 1. Introduction

The inclusion of functional traits in the analysis of biodiversity is improving our understanding on how species and communities vary in time and space, how they interact and which conservation risks they face (McGill et al., 2006; Gilman et al., 2010). In particular, ecophysiological traits provide inference on the species' fundamental niche, overcoming the effects of biotic interactions and dispersal (Sillero, 2011). If fundamental niche of a given species can be consistently assessed, predicting its responses under novel environments will be more reliable (Kearney et al., 2010). Because of that, ecophysiological information is gaining relevance in macroecology and risk assessment, particularly for small ectotherms which are largely sedentary and directly exposed to local climate variations (Chown and Gaston, 2008; Žagar et al., 2017). In this context, the analysis of the ecophysiology in those species living under extreme environmental conditions in terms of

humidity and temperature may shed light on the expected responses by species from more mesic environments will face in the future if climate change scenarios, dominated by warming and aridification, are confirmed (Huey et al., 2012).

In arid environments water availability and extreme temperatures are crucial factors controlling biological processes of organisms, affecting their diversity and abundance (Whitford, 2002). However, disentangling their effects on a given species in practice reveals difficult since their variation in nature is generally associated and effects on organisms may be interactive. Hence, not only field surveys but also experimental evidence is needed. In this context desert coleopterans constitute excellent model organisms. This is highly successful group which combines several phenotypic adaptations to survive in this restrictive environment in terms of temperature and humidity (Cloudsley-Thompson, 2001). Remarkably, they can be locally abundant, especially during the rare humid episodes taking place in desert ecosystems

\* Corresponding author.

E-mail address: [carretero@cibio.up.pt](mailto:carretero@cibio.up.pt) (M.A. Carretero).

**Table 1**

Number of specimens, body mass ( $m_b$ ), body temperature ( $T_b$ ), substrate temperature ( $T_s$ ) and air temperature ( $T_a$ ), and recorded per species and sex in the Llanos de Challe National Park (Atacama region of Chile). The values correspond to the mean, the standard deviation and maximum and minimum value.

Mean $\pm$ SE Min – Max	<i>Gyriosomus kingi</i>		<i>Gyriosomus planicollis</i>	
	males ( $n = 95$ )	females ( $n = 93$ )	males ( $n = 27$ )	females ( $n = 33$ )
Mb (g)	0.51 $\pm$ 0.01 0.3–0.7	1.07 $\pm$ 0.02 0.8–1.6	0.42 $\pm$ 0.02 0.2–0.6	0.84 $\pm$ 0.03 0.7–1.3
Tb (°C)	31.88 $\pm$ 0.48 20.40–39.52	33.02 $\pm$ 0.50 21.96–40.66	32.88 $\pm$ 0.73 25.49–39.52	33.90 $\pm$ 0.64 23.62–39.00
Ts (°C)	36.18 $\pm$ 0.85 21.23–54.79	36.65 $\pm$ 0.81 22.89–54.27	36.67 $\pm$ 1.20 27.3597–49.80	38.24 $\pm$ 1.25 22.16–52.40
Ta (°C)	23.25 $\pm$ 0.31 16.76–29.65	23.29 $\pm$ 0.30 17.90–31.00	24.01 $\pm$ 0.60 18.839–29.23	24.09 $\pm$ 0.58 18.63–30.89

(Cloudsley-Thompson, 1991), then providing a unique opportunity for record both field and experimental data.

In the transitional coastal desert of Chile (latitude 25–32° S), the irregular precipitations above 150 mm combined with appropriate temperature and light conditions may cause an increase in primary production, mainly of short-lived geophytes (Gutiérrez, 2008). This event, which represents the humid phase of the coastal desert (flowering desert), causes a direct or indirect increase in the population size of numerous taxa by activating their halted biological cycles (latency, diapause), triggering reproductive events (Armesto et al., 1993), or causing population outbreaks (Cepeda-Pizarro et al., 2007; Pizarro-Araya et al., 2015). The epigean tenebrionid beetles from the genus *Gyriosomus* (Cepeda-Pizarro et al., 2005a, 2005b) represent an endemic and eremic group from Chile with 38 species described to date. Approximately 90% of the genus diversity is distributed across coastal dunes and plains of the Atacama and Coquimbo regions (Pizarro-Araya and Jerez, 2004; Pizarro-Araya and Flores, 2004). *Gyriosomus* populations tend to increase during the humid phase of the coastal desert, contributing to plant resource fragmentation and nutrient cycles (Cepeda-Pizarro et al., 2005a, 2005b), and serving as a key trophic resource for reptiles and mammals (Castro et al., 1991; Pizarro-Araya, 2010; Valladares Faúndez et al., 2015).

Despite this pivotal role, studies on *Gyriosomus* have focused mainly on taxonomical (Mondaca, 2004; Pizarro-Araya and Flores, 2004), bionomics (Pizarro-Araya et al., 2005, 2007, 2011), biogeographical (Pizarro-Araya and Jerez, 2004), and general ecological aspects (Cepeda-Pizarro et al., 2005a, 2005b; Pizarro-Araya, 2010; Alfaro et al., 2009, 2016), whereas physiology and ethology (Vidal et al., 2011) have been largely neglected. However, both are relevant to interpret their temporal and spatial abundance and distribution (Bozinovic, 2002). As other desert ectotherms adult *Gyriosomus* are directly exposed to the physical restrictions prevailing in such environments, namely strong thermal variations and the limited availability of free water (Cloudsley-Thompson, 2001). To maintain their water balance and body temperature within an optimum range, these organisms possess a combination physiological, behavioral, and morphological strategies (Cloudsley-Thompson, 1988).

In this context, we conducted an integrated analysis of the activity patterns and the thermal and hydric biology of two *Gyriosomus* species living sympatrically in a dune ecosystem of the coastal area of the Atacama region of Chile (Pizarro-Araya and Jerez, 2004; Cepeda-Pizarro et al., 2005a). These species can be considered representing the extreme of an environmental shift in global climate that is affecting most small terrestrial ectotherms. By understanding the physiological and behavioral mechanisms used by these species in arid conditions we intend to infer the responses, and vulnerabilities, of small ectotherms to climate change. As such, we examined the activity pattern, body temperatures and water loss rates considering species and sex while taking body size into account. Here we postulate that the water loss rate, traded off with body temperature and determined by body mass, would be the main factor restricting the diurnal activity. In this way small

ectotherms should restrict epigean activity to those hours when thermal costs are lower, namely, reducing evaporative water loss at very high temperatures and, hence, maintaining a positive water balance.

## 2. Materials and methods

### 2.1. Study site

The study was conducted in the Llanos de Challe National Park (28°11'02.7" S; 71°09'18.9" W, 30 m.s.l.; Atacama region, Chile). This area is part of the plant formation of the coastal desert of Huasco (Gajardo, 1993), included in the transitional coastal desert of Chile (latitude 25–32° S) (Cepeda-Pizarro et al., 2005a, 2005b). The climate in the area is semiarid subtropical Mediterranean in the northern margin and marine subtropical Mediterranean in the southern margin (Novoa and Villaseca, 1989). The total precipitation recorded in the study area (Huasco Bajo Station 20°20'21" S; 71°11'35" W, 50 m.s.l) in 2015 was 50.5 mm and was concentrated in July (11 mm), August (37 mm), and October (2.5 mm) (DGA, 2016).

### 2.2. Study species

*Gyriosomus kingi* Reed, 1873, and *Gyriosomus planicollis* Gebien, 1944 are two tenebrionid species widely distributed along the Atacama region from Hacienda Castilla - Llanos de Challe National Park (27°53'–28°11' S) to Travesía - Freirina (27°32'–28°30' S). Both species live in sympatry and syntopy in dune ecosystems of the coastal area of the Atacama region of Chile (Pizarro-Araya and Jerez, 2004; Cepeda-Pizarro et al., 2005a). They are univoltine, have their last larval stage in diapause (Cepeda-Pizarro et al., 2005a) and emerge after rainfall episodes. Morphologically, both species differ in size (Cepeda-Pizarro et al., 1996), with *G. kingi* (mean length 17.86 mm) being larger than *G. planicollis* (mean length 16.72 mm). At intraspecific level they are both characterized by their notorious sexual dimorphism where females are larger than males (Cepeda-Pizarro et al., 1996; see also Table 1).

### 2.3. Censuses

A total of 188 specimens of *G. kingi* (95 males; 93 females) and 60 specimens of *G. planicollis* (27 males; 33 females) were captured in a random walking route during a single uninterrupted sampling effort conducted between 8.30 a.m. and 9.00 p.m. in the spring of 2015. The study site covered an area of 105 ha, which was traveled through 100-meter walking routes arranged in a parallel manner according to Vidal et al. (2011).

For each captured specimen we recorded the specimen's sex (based on sexual secondary characters) and body mass (Digital Scale, Model 1108-5;  $\pm 0.01$  g) together with the time of the day. To prevent pseudoreplication all measured individuals were marked using an indelible pen.

**Table 2**

GLM comparisons of the subelytral body temperatures (T<sub>b</sub>) between species and sexes of *Gyriosomus* spp. from the Llanos de Challe National Park (Atacama region of Chile); and GLM using the substrate (T<sub>s</sub>) and air (T<sub>a</sub>) temperatures as well as the body.

	Mb			Ts			Ta		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
<b>GLM</b>									
Species	1, 244	56.70	< 10 <sup>-6</sup>	1, 244	1.31	0.25	1, 244	2.77	0.10
Sex	1, 244	608.21	< 10 <sup>-6</sup>	1, 244	0.69	0.41	1, 244	0.02	0.89
Species*sex	1, 244	0.66	0.41	1, 244	0.11	0.75	1, 244	< 10 <sup>-4</sup>	0.93
<b>GLM Tb</b>									
Species	1, 244	2.30	0.14						
Sex	1, 244	2.20	0.13						
Species*sex	1, 244	0.01	0.93						
<b>GLM Tb (Ts, Ta)</b>									
Species	1, 242	0.46	0.50						
Sex	1, 242	4.08	0.04						
Species*sex	1, 242	0.47	0.49						
<b>GLM Tb (Ts, Ta, Mb)</b>									
Species	1, 241	0.11	0.74						
Sex	1, 241	4.33	0.04						
Species*sex	1, 241	0.008	0.93						

Mass (Mb) as continuous predictors. These variables were log-transformed.

#### 2.4. Active body temperatures and ambient temperatures

For each specimen collected, we recorded the subelytral cavity temperature (T<sub>b</sub>), as an equivalent of body temperature, within five second since the capture. In addition we recorded soil temperature (T<sub>s</sub> in contact with the soil) and air temperature (T<sub>a</sub> 10 cm above the soil) (Duncan, 2003; Vidal et al., 2011). Measurements were obtained using a digital thermometer (4 ch K 88598) connected to a type-K thermocouple (copper-constantan) 0.5 mm in diameter that was introduced at a depth of 1 cm in the subelytral cavity (precision  $\pm 0.1$  °C). Both the digital thermometer and the thermocouple were previously calibrated in the laboratory.

#### 2.5. Ambient temperature

Temperatures (substrate and air) were recorded every 15 min in the study site using four HOBO dataloggers (ProV2) equipped with two probes each. The thermal variations in the habitat during the study period were derived from these records. The dataloggers were randomly set in the sampling area, in microhabitats that were similar to the sites where the coleopterans were recorded. One of the probes remained in contact with the substrate while the other was suspended 10 cm above the soil (in the air).

#### 2.6. Water loss rates

During the same study period, a random sample of 48 individuals from each species, representing both sexes according to their abundance in the field was captured, weighed, and kept individually in a 100 cc plastic box containing a 5 cm layer of sand. The specimens were transferred to the Laboratory of Ecophysiology of the University of Atacama (Chile) and kept under a natural photoperiod at a temperature of  $26 \pm 0.5$  °C, and supplied with water (via a soaked sponge) and *Erodium* sp. (Geraniaceae) for one week (acclimation).

Water loss was determined gravimetrically. A total of 48 individuals of each species previously deprived of food for 3 days (*G. kingi*: 24 males and 24 females; *G. planicollis*: 36 males and 9 females) were individually placed in 25 mL translucent plastic tubes. Each tube had perforated walls and one of its end covered with a mesh for ventilation. The tubes were put in groups of 12 inside a desiccator at a temperature of  $26 \pm 0.6$  °C. The relative humidity inside the desiccator was kept at

25% using CaSO<sub>4</sub> and silica gel. Both variables were recorded with a HOBO H08-003-02 datalogger. Each specimen had their body mass (M<sub>b</sub>) measured at one hour intervals, for six hours, using a Vibra scale (LF224R; Max/d 220/  $\pm 0.1$  mg). Energy demands of coleopterans during this short period are reduced; hence, most weight loss is attributed to evaporation (Harrison et al., 2012). Water loss ratio was calculated based on the following formula: (M<sub>b,t</sub> – M<sub>b,t+1</sub>)/M<sub>b,0</sub>, where M<sub>b,t</sub> is the mass measured in the time interval t; M<sub>b,t+1</sub> is the mass measured in the time interval t + 1, and M<sub>b,0</sub> is the body mass measured at the start of the experiment. The overall water loss rate was obtained from the two lowest values of each experimental run and expressed as mg/g/h.

#### 2.7. Statistical analyses

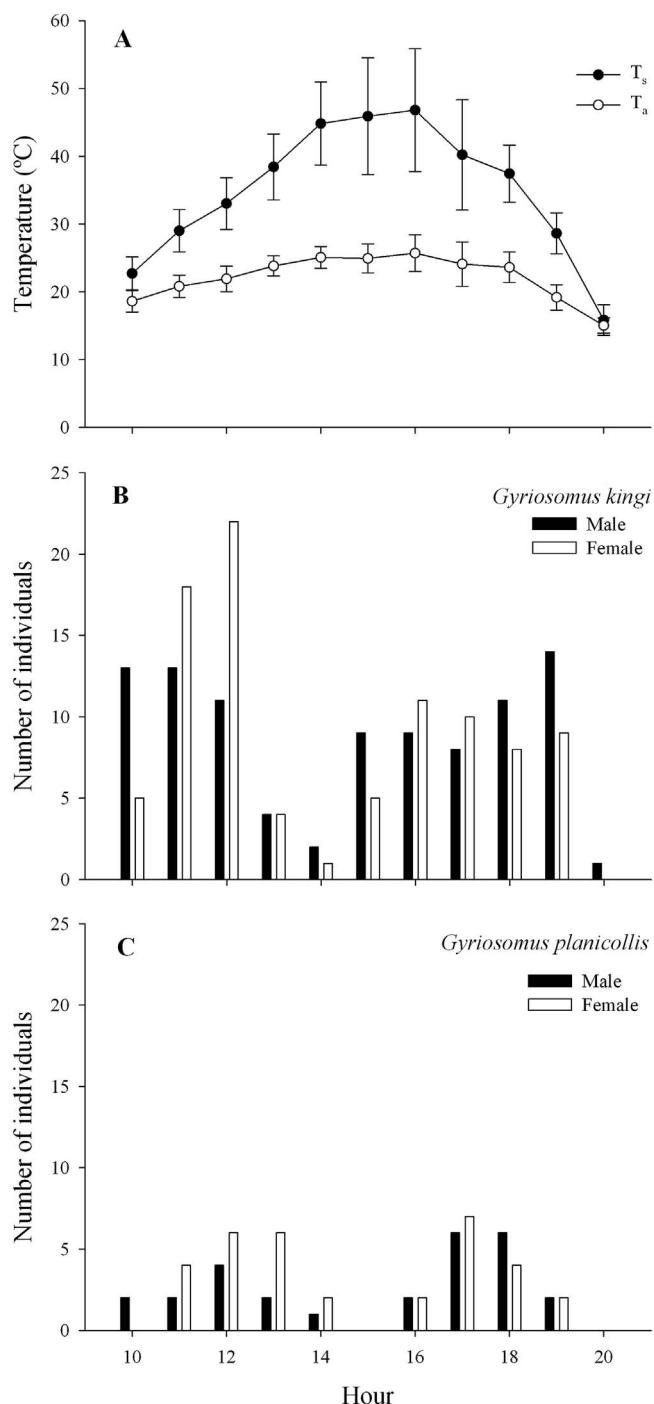
The temperatures recorded with the dataloggers (T<sub>s</sub> and T<sub>a</sub>) were log-transformed compared using a Two-way ANOVA with hour and substrate/air as factors. Afterwards, multiple comparisons were conducted by Tukey test (Zar, 1984). Activity patterns between species and sexes were compared by means of log-linear analysis (Jobson, 1992). The mean T<sub>b</sub>, mean Mb and mean water loss ratio (of the two lowest values, TWL) were compared using General Linear Models (GLM).

The thermoregulatory capacities (Huey and Slatkin, 1976) were assessed by fitting a regression line to the relations between T<sub>s</sub> and T<sub>b</sub>, and T<sub>a</sub> and T<sub>b</sub>. Since, relations deviated from a straight line (see results), variables were log-transformed to ensure homoscedasticity and normality. Analyses were performed using R (R Development Core Team, 2008) packages EZR (Kanda, 2012) and R-Commander (Fox, 2005), as well as Statistica 13.2 (Dell Inc, 2016).

### 3. Results

A total of 248 specimens were collected during the sampling period (Table 1). As expected *G. kingi* attained large body sizes than *G. planicollis* while females were bigger than males regardless the species. However, sexual size dimorphism was more pronounced in *G. kingi* than in *G. planicollis* (Tables 1 and 2).

The mean soil and air temperatures recorded uninterruptedly with the dataloggers were 35.29 °C (Min = 15.6; Max = 28.5; SD = 11.06) and 22.23 °C (Min = 16.2; Max = 53.6; SD = 3.77), respectively. These values differed through time and between air and soil with a



**Fig. 1.** Records of temperature (substrate  $T_s$  and air  $T_a$ , A) and frequency of activity of *Gyriosomus* spp. individuals in the Llanos de Challe National Park (Atacama region, Chile; B and C). The values correspond to the mean and the standard deviation.

significant interaction between both factors (soil/air  $F_{1,280} = 689.56$ ,  $p < 10^{-6}$ ; hour  $F_{1,280} = 59.94$ ,  $p < 10^{-6}$ ; soil/air \*hour  $F_{11,280} = 15.27$ ,  $p < 10^{-6}$ ). Soil not only attained higher values than air but also was more variable (Fig. 1). The highest temperatures were recorded in soil between 14h00 and -17h00 ( $p < 0.05$ ). The lowest temperatures were recorded in soil at 9h00 and air at 9h00 and 20h00 (Fig. 1).

Diel activity, as estimated from the number of individuals detected in the random walks, was bimodal regardless the species and sex, peaking in mid-morning and mid-afternoon but decreasing in the middle of the day (Fig. 1). Nevertheless, log-linear models detected

**Table 3**

Results of the log-linear analyses of the influences of species, sex and time interval (1 h) on the activity pattern of *Gyriosomus* spp. from the Llanos de Challe National Park (Atacama region of Chile). Significant results in bold.

	d.f.	Partial $\chi^2$	P	Marginal $\chi^2$	P
<b>species</b>	1	<b>63.19</b>	< 0.10 <sup>-6</sup>		
<b>sex</b>	1	0.06	0.81		
<b>time</b>	10	<b>67.16</b>	< 0.10 <sup>-6</sup>		
<b>species*sex</b>	1	0.11	0.74	0.47	0.49
<b>species*time</b>	10	<b>19.19</b>	0.04	<b>19.54</b>	<b>0.03</b>
<b>sex*time</b>	10	15.37	0.12	15.72	0.11
Log-linear model (factors)	Test		Value	d.f.	P
automatic (species*time)	Max. likelihood $\chi^2$ Pearson $\chi^2$	17.08 16.61	22	22	0.76 0.78

differences between species, *G. planicollis* tending to be less active during midday than *G. kingi*, but not between sexes within the same species (Table 3).

Raw plots of body temperature versus soil and air temperatures deviated from a straight line for both species and sexes. In fact, the relation between both body and environmental temperature fitted better to a logarithmic curve with the slope gradually declining with the increasing temperature ( $p < 0.001$ , Fig. 2). In all the cases the deviation was more marked for the  $T_b$  vs.  $T_s$  relationship. In other words, coleopterans tended thermoconformed less with increasing substrate temperatures and simply disappeared at extremely high temperatures (Figs. 1 and 2). This was less evident for air temperature. Nonetheless, no major statistical differences were found between the regression curves of  $T_s$  vs.  $T_b$  of sexes and species (GLM,  $p > 0.05$ ), all following the same trend. Accordingly, no significant differences either between species, between sexes or interaction between both factors were observed in the mean active body temperatures (Table 2). Such result persisted after accounting for substrate and air temperatures and body mass (sex was here marginally significant).

On the other hand, water loss rates obtained for *G. kingi* were 6.31 mg/g/h ( $SD = 1.73$ ) and 4.43 mg/g/h ( $SD = 1.90$ ) in males and females, respectively (Fig. 3). These values were significantly higher in *G. planicollis* than in *G. kingi* and in females compared to males but there was no interaction between species and sex (species  $F_{1,90} = 22.52$ ,  $p = 8 \times 10^{-6}$ ; sex  $F_{1,90} = 15.59$ ,  $p = 0.0002$ ; species\*sex  $F_{1,90} = 0.007$ ,  $p = 0.93$ ). Since water loss decreased logarithmically with body mass (Fig. 3), water loss differences between sexes disappeared after accounting for body mass but small but statistically significant interspecific difference remained, namely higher relative water loss in *G. planicollis* (species  $F_{1,89} = 5.57$ ,  $p = 0.02$ ; sex  $F_{1,89} = 0.48$ ,  $p = 0.49$ ; species\*sex  $F_{1,90} = 4.36$ ,  $p = 0.04$ ).

#### 4. Discussion

Ecophysiological results were complex but in general corroborated our expectations pointing to a trade-off between hydric and thermal ecology although, such trade-off was partial and restricted to the high range of temperatures. More interestingly, behavioral (activity) and ecophysiological (body temperature and water loss rates) responses were strongly determined by body size with species and sex playing only a subsidiary role and, hence, suggesting a general trend.

It is well known that temperature and water availability are the main environmental variables responsible for the abundance and distribution of insects (Chown and Nicolson, 2004). In ectotherms, the biological functions depend on the environment's thermal load; for this reason, activity rhythms in diurnal species are strongly affected by ambient temperature (Angilletta, 2009). Regarding water, it has been proposed that tenebrionid coleopterans have three physiological

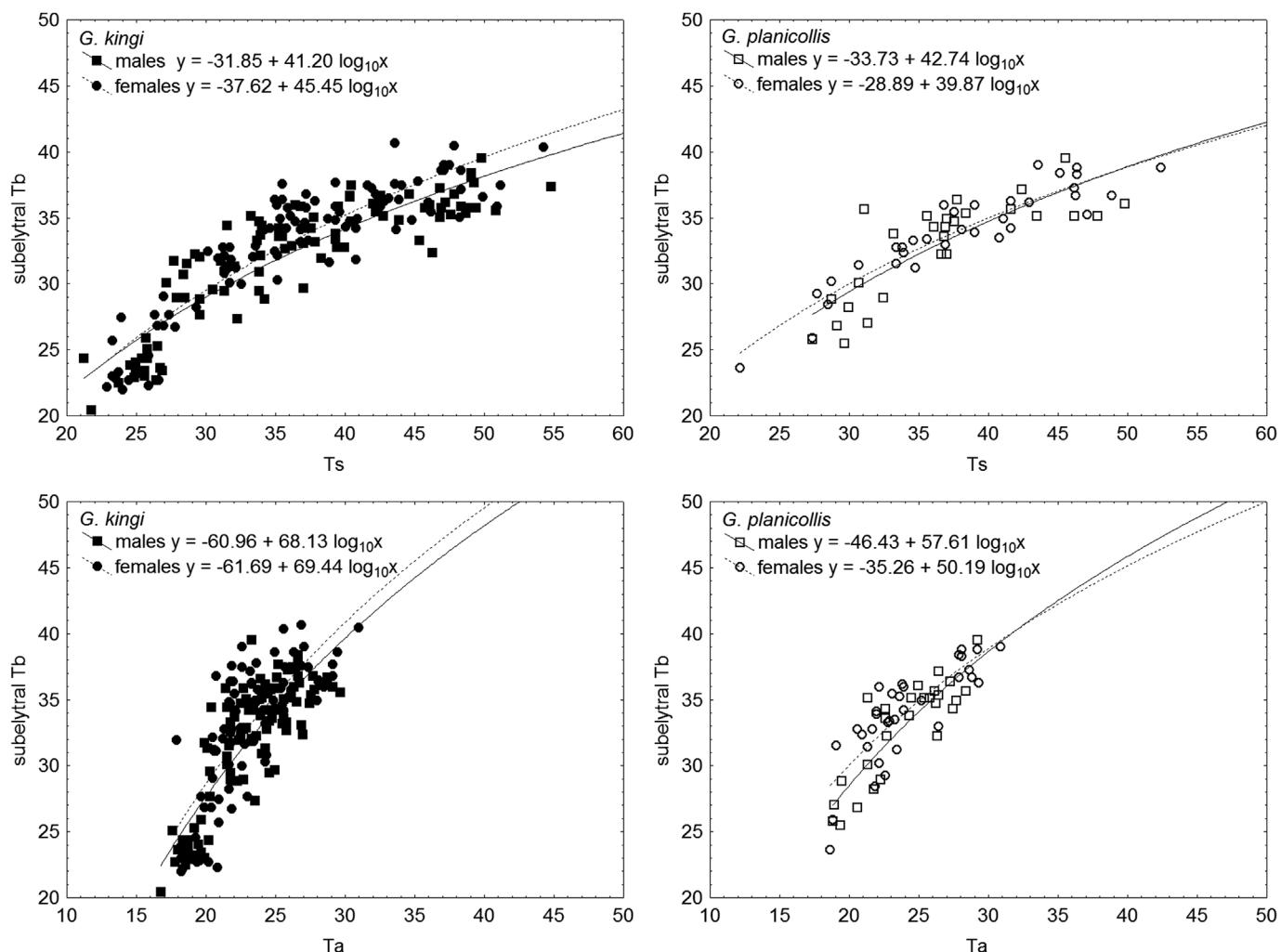


Fig. 2. Logarithmic regression between body temperature and substrate and air temperatures in male (squares) and female (circles) *Gyriosomus kingi* (closed symbols) and *Gyriosomus planicollis* (open symbols).

strategies to cope with water loss in arid ecosystems, namely, reduction in cuticular water permeability, reduction in respiratory water loss thanks to a closed subelytral cavity, and reduction in metabolic rate (Harrison et al., 2012). The latter would imply selection for lower

active body temperatures (Zachariassen et al., 1987; Zachariassen, 1991). Similarly, the small size of these organisms may imply less water storage capacity and higher water loss due to their large surface area/volume ratio (Kühnel et al., 2017) as well as a low dispersion capacity

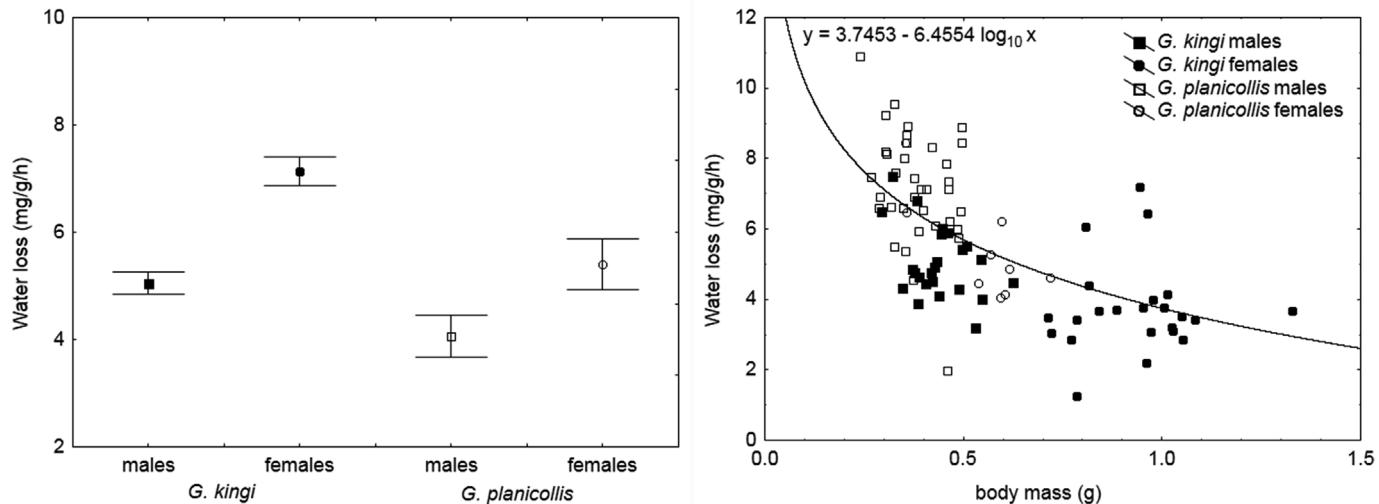


Fig. 3. Mean water loss ( $\pm \text{SD}$ ) in male and female (left) and logarithmic regression between water loss and body mass in *Gyriosomus* spp.

for searching for proper microhabitats. According to this, several mechanisms, ranging from molecular to systemic ones, in combination with evasive behaviors, would allow many species to survive in arid and semiarid environments (Somme, 1995).

Our results show that the *Gyriosomus* species studied here follow similar trends in thermal and hydric ecophysiology and diel activity. Remarkably, in the study site, these coleopterans were exposed to temperatures above 55 °C. Additionally, free water in these habitats is scarce or nonexistent and is usually associated to plant species that are part of the coleopterans' diet (Pizarro-Araya, 2010). Both *G. kingi* and *G. planicollis* are univoltine species whose larvae end diapause during the humid phase of the Atacama Desert. During this period, they feed on short-lived vegetation, reproduce, and eventually die at the end of the humid phase. Being ectothermic diurnal species, both coleopterans have to consume resources during the day with the risk of suffering from hyperthermia, dehydration, and predation (Vidal et al., 2011). An important component in the biology of *G. kingi* and *G. planicollis* is their evasive behavior, which is reflected in their diurnal activity patterns. Frequencies of activity drop considerably, and even stop, during hours when the thermal load reaches 40–60 °C, as is the case with the smaller *G. planicollis*. The resulting pattern is bimodal, and it is reported as one of the most important strategies used by coleopterans in the Kalahari Desert (Cloudsley-Thompson, 1991) and is shared by other species of this genus (Vidal et al., 2011). Field observations conducted during this study showed that both species avoid extremely high temperatures by sheltering themselves under shrubs from the genera *Nolana divaricata* (Lindl.) I.M. Johnst. (Nolanaceae), *Tetragonia maritima* Barnéoud (Aizoaceae) and *Oxalis gigantea* Barnéoud (Oxalidaceae), and geophytes from the genus *Rhodophiala* (Amaryllidaceae). This reinforces the idea that evasive behavior may be one of the main strategies in tenebrionids (Ahearn, 1971; Edney, 1971) and most small ectotherms (Cloudsley-Thompson, 1991) from xeric zones.

On the other hand, water loss rates were higher in smaller individuals, regardless of the species or sex, compared to larger ones, which is likely the result of their higher mass/volume ratio (Schmidt-Nielsen, 1984). In this respect, diurnal activity and body size may considerably affect water loss on insects (Hadley, 1994; Duncan et al., 2002), where differences in the survival of males and females under arid conditions would depend on higher tolerance to desiccation, which is strongly associated to body size (Renault and Coray, 2004). These differences may condition males of both species to start their activity before conspecific females and *G. planicollis* to start earlier than *G. kingi* as well as to reduce it in order to avoid high temperatures during hours with high thermal load, as observed during this study. Nevertheless, *G. planicollis* still lost slightly more water than *G. kingi* after accounting for its smaller size, suggesting taxonomic influence even if minor when compared to the effect of body size.

Contrary to expectations, we failed to detect differences in active body temperature, which was expected to be lower in *G. planicollis* and in males of both species as a way to prevent desiccation. In absence of other evidence, we tentatively interpret this as a phylogenetic signal, suggesting that this thermal variable would have been preserved in the evolution of the group, only adjusting activity according to local environment. However, that similarity might also derive from sharing similar microhabitats although we would still expect different activity costs in terms of water loss. On the other hand both sexes may also face difference fitness costs in terms associated to sexual and fecundity selection (Punzo, 2000). Taking into consideration that mean active body temperatures of 25.25 °C and 27.2 °C have been documented for *G. subrugatus* and *G. batesi* (Vidal et al., 2011), broader comparative studies across multiple species and between sexes are needed to confirm any of these hypotheses.

The logarithmic relation between body and environmental temperatures suggests a two-step strategy. Coleopterans mostly acted as thermoconformers (Angilletta, 2009) at a wide range of low and medium environmental temperatures but they gradually tended to

select lower body temperatures than expected at very high environmental temperatures particularly regarding the substrate. Therefore, in the thermoconformer step coleopterans followed the environmental temperature, deflecting the energy saved from thermoregulation to feeding and reproduction. Although this is common in ectotherms from many environments, it seems especially crucial during the short humid phase of the Atacama Desert (Cepeda-Pizarro et al., 2005a). In the "thermoregulatory" step, beetles are probably displaying an emergency response to prevent not only overheating but also desiccation. Such complex interactions between thermal and hydric ecology clearly deserve further experimental work to determine which takes precedence and under which environmental conditions.

In conclusion, the responses of these two coleopterans living at the ecophysiological edge in Atacama desert not only confirm previous findings that water availability may take precedence on the temperature as environmental constraint for invertebrates in arid ecosystems (Punzo, 2000) but also point to new directions with implications in climate change inference. Namely, body size mediated the behavioral and ecophysiological responses found here. The smallest individuals were more vulnerable to desiccation, could not attain the highest temperatures and have to remain inactive, which involves associated costs in terms of foraging, social interactions and breeding (Harrison et al., 2012). Since this effect was insensitive to species and sex, a general negative trend for small ectotherms is suggested. On the other hand, the relationships between hydric and thermal ecophysiology were tight but complex. After our results, general increase in environmental temperature will certainly narrow the activity window, especially for small individuals. However, if such warming is accompanied by a severe decrease in water availability, such activity restriction will be larger and associated impacts will be magnified. This advocates for not neglecting hydric traits in climate change forecasts for small ectotherms (Kearney et al., 2009; Riddell et al., 2017) despite the intrinsic uncertainty of the predictions for the corresponding environmental proxies (i.e. precipitation, evapotranspiration, humidity, Hijmans et al., 2005). Overall, the ecophysiology of two modest Atacama beetles provides insights on the biology and conservation not only for other desert invertebrates but also for their relatives inhabiting milder environments but threatened by global change (Chown and Gaston, 2008).

## Acknowledgments

Our acknowledgements to CONAF for granting permission and facilities to work in the Llanos de Challe National Park (Projects N. 028/2015 and 053/2015), and especially to Isla Troncoso, Sergio Araya, Alberto Villegas and Fernando Mercader. We also thank Hector Muñoz for his important technical support in laboratory. Funding for this research was provided by the incubation projects of the Faculty of Natural Sciences of the University of Atacama (Res. Ex. 2015) (CT), the regular 16/05 DIUDA project of the University of Atacama (CT), and by grants from DIULS PR15121/VACDDI001 project of the University of La Serena, La Serena, Chile (JPA). MAC is supported by project NORTE-01-0145-FEDER-000007. We thank four anonymous reviewers for their suggestions on an early draft of this manuscript.

## References

- Ahearn, G.A., 1971. Ecological factors affecting population sampling of desert tenebrionid beetles. *Am. Mid. Nat.* 86, 385–406.
- Alfaro, F.M., Pizarro-Araya, J., Flores, G.E., 2009. Epigean tenebrionids (Coleoptera: Tenebrionidae) from the Choros archipelago (Coquimbo region, Chile). *Entomol. News* 120, 125–130.
- Alfaro, F.M., Pizarro-Araya, J., Flores, G.E., 2016. Composición y estructura del ensamblaje de tenebrionidos epigeos (Coleoptera: Tenebrionidae) de ecosistemas continentales e insulares del desierto costero transicional de Chile. *Rev. Mex. Biodivers.* 87, 1283–1291.
- Angilletta, M., 2009. Thermal adaptation: a Theoretical and Empirical Synthesis. Oxford University Press Inc., New York, USA.

- Armesto, J.J., Vidiella, P.E., Gutiérrez, J.R., 1993. Plant communities of the fog-free coastal desert of Chile: plant strategies in a fluctuating environment. Rev. Chil. Hist. Nat. 66, 271–282.
- Borzinovic, F., 2002. Fisiología ecológica y evolutiva: Teoría y casos de estudio en animales. Ediciones Universidad Católica de Chile, Santiago, Chile.
- Castro, S.A., Jiménez, J.E., Jaksic, F.M., 1991. Diet of the racerunner *Callopistes palluma*, in north-central Chile. J. Herpetol. 25, 127–129.
- Cepeda-Pizarro, J.G., Vásquez, H., Veas, H., Colon, G., 1996. Relaciones entre tamaño corporal y biomasa en adultos de Tenebrionidae (Coleóptera) de la estepa costera del margen meridional del desierto chileno. Rev. Chil. Hist. Nat. 69, 67–76.
- Cepeda-Pizarro, J., Pizarro-Araya, J., Vásquez, H., 2005a. Composición y abundancia de artrópodos epígeos del Parque Nacional Llanos de Challe: impactos del ENOS de 1997 y efectos del hábitat pedológico. Rev. Chil. Hist. Nat. 78, 635–650.
- Cepeda-Pizarro, J., Pizarro-Araya, J., Vásquez, H., 2005b. Variación en la abundancia de la artrópodo-fauna, con énfasis en tenebrionídos epígeos, del desierto costero transicional de Chile. Rev. Chil. Hist. Nat. 78, 651–663.
- Cepeda-Pizarro, J., Vega, S., Vásquez, H., Elgueta, M., Pizarro-Araya, J., 2007. Demography of two populations outbreaks of *Elasmoderus wagenknechti* (Orthoptera: Tristiridae) in the semiarid region of Chile. Neotrop. Entomol. 36, 495–502.
- Chown, S.L., Gaston, K.J., 2008. Macrophysiology for a changing world. Proc. R. Soc. Lond. Ser. B 275, 1469–1478.
- Chown, S.L., Nicolson, S.W., 2004. Insect Physiological Ecology. Mechanisms and Patterns. Oxford University Press, Oxford.
- Cloudsley-Thompson, J.L., 1988. Evolution and Adaptation of Terrestrial Arthropods. Springer, Berlin Heidelberg New York.
- Cloudsley-Thompson, J.L., 1991. Ecophysiology of Desert Arthropods and Reptiles. Springer-Verlag, Berlin.
- Cloudsley-Thompson, J.L., 2001. Thermal and water relations of desert beetles. Naturwissenschaften 88, 447–460.
- DGA, 2016. Dirección General de Aguas. <http://snia.dga.cl/BNAConsultas/reportes>, Accessed date: 16 November 2016.
- Duncan, F.D., 2003. The role of the subelytral cavity in respiration in a tenebrionid beetle, *Onymacris multistriata* (Tenebrionidae: Adesmiini). J. Insect Physiol. 49, 339–346.
- Duncan, F.D., Krasnov, B., McMaster, M., 2002. Metabolic rate and respiratory gas-exchange patterns in tenebrionid beetles from the Negev Highlands, Israel. J. Exp. Biol. 205, 791–798.
- Edney, E.B., 1971. The body temperature of tenebrionid beetles in the Namib Desert of Southern Africa. J. Exp. Biol. 55, 253–272.
- Fox, J., 2005. The R commander: a basic-statistics graphical user interface to R. J. Stat. Softw. 14, 1–42.
- Gajardo, R., 1993. La Vegetación Natural de Chile. Clasificación y Distribución Geográfica. Editorial Universitaria, Santiago.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends Ecol. Evol. 25, 325–331.
- Gutiérrez, J.R., 2008. El desierto florido de la Región de Atacama. In: Squeo, F.A., Arancio, G., Gutiérrez, J.R. (Eds.), Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su Conservación: Región de Atacama. Universidad de La Serena, La Serena, pp. 285–291.
- Hadley, N.F., 1994. Water Relations of Terrestrial Arthropods. Academic Press, San Diego.
- Harrison, J.F., Woods, H.A., Roberts, S.P., 2012. Ecological and Environmental Physiology of Insects. Oxford University Press, Oxford.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.
- Huey, R.B., Slathkin, M., 1976. Cost and benefits of lizard thermoregulation. Quaterly Rev. Biol. 51, 363–384.
- Huey, R.B., Kearney, M., Krokenberger, A., Holtum, J.A.M., Jess, M., Williams, S.E., 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos. Trans. R. Soc. B 367, 1165–1679.
- Dell Inc, 2016. Dell Statistica (Data Analysis Software System), Version 13 ([software.dell.com](http://software.dell.com)) .
- Jobson, J.D., 1992. Applied Multivariate Data Analysis. Volume II: Categorical and Multivariate Methods. Springer, New York.
- Kanda, Y., 2012. Free statistical software: EZR (Easy R) on R commander. Available from: <http://www.jichi.ac.jp/saitama-sct/SaitamaHP.files/statmedEN.html>, Accessed date: 21 October 2016.
- Kearney, M., Porter, W.P., Williams, C., Ritchie, S., Hoffmann, A.A., 2009. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. Funct. Ecol. 23, 528–538.
- Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B., 2010. Modelling the ecological niche from functional traits. Philos. Trans. R. Soc. Londong B 346, 3499–3483.
- Kühnel, S., Brückner, A., Schmelzle, S., Heethoff, M., Blüthgen, N., 2017. Surface area–volume ratios in insects. Insect Sci. 24, 829–841.
- McGill, B.J., Enquist, M., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.
- Mondaca, J., 2004. Nueva especie de *Gyriosomus* Guérin-Méneville, 1834 (Coleóptera: Tenebrionidae: Nycteliini) del extremo norte de la Región de Atacama (Chile). Rev. Chil. Entomol. 30, 21–26.
- Novoa, S.A., Villaseca, S., 1989. Mapa agroclimático de Chile Investigaciones Agropecuarias. INIA, Santiago, Chile.
- Pizarro-Araya, J., 2010. Hábitos alimenticios del género *Gyriosomus* Guérin-Méneville, 1834 (Coleóptera: Tenebrionidae): qué comen las vaquitas del desierto costero? Idesia 28, 115–119.
- Pizarro-Araya, J., Flores, G.E., 2004. Two new species of *Gyriosomus* Guérin-Méneville from the Chilean coastal desert (Coleóptera: Tenebrionidae: Nycteliini). J. N. Y. Entomol. Soc. 112, 121–126.
- Pizarro-Araya, J., Jerez, V., 2004. Distribución geográfica del género *Gyriosomus* Guérin-Méneville, 1834 (Coleóptera: Tenebrionidae): una aproximación biogeográfica. Rev. Chil. Hist. Nat. 77, 491–500.
- Pizarro-Araya, J., Jerez, V., Cepeda-Pizarro, J., 2005. Descripción de huevos y larvas de primer estadio del género *Gyriosomus* Guérin-Méneville, 1834 (Coleóptera: Tenebrionidae: Nycteliini). Gayana 69, 277–284.
- Pizarro-Araya, J., Jerez, V., Cepeda-Pizarro, J., 2007. Reproducción y ultraestructura del huevo y larva de primer estadio de *Gyriosomus kingi* (Coleóptera: Tenebrionidae) del desierto de Atacama. Rev. Biol. Trop. 55, 637–644.
- Pizarro-Araya, J., Jerez, V., Cepeda-Pizarro, J., Alfaro, F.M., 2011. Caracteres pre-imaginarios y aspectos bionómicos de *Gyriosomus luczoti* Laporte, 1840 (Coleóptera: Tenebrionidae), elemento endémico y erémico del desierto costero chileno. Animal Biodivers. Conserv. 34, 265–272.
- Pizarro-Araya, J., Cepeda-Pizarro, J., Mondaca, J., Cortés-Contreras, M., 2015. A population outbreak of *Lichnia gallardoi* Gutiérrez, 1943 (Coleóptera: scarabaeidae) in the matorral shrublands of the transitional coastal desert of Chile. Coleopterist. Bulletin 69, 337–340.
- Punzo, F., 2000. Desert Arthropods: Life History Variations. Springer-Verlag, Heidelberg.
- R Development Core Team, 2008. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria 3-900051-07-0. <http://www.R-project.org>.
- Renault, D., Coray, Y., 2004. Water loss of male and female *Alphitobius diaperinus* (Coleóptera: Tenebrionidae) maintained under dry conditions. Eur. J. Entomol. 101, 491–494.
- Riddell, E.A., Apanovitch, E.K., Odom, J.P., Sears, M.W., 2017. Physical calculations of resistance to water loss improve predictions of species range models. Ecol. Monogr. 87, 21–33.
- Schmidt-Nielsen, K., 1984. Scaling: Why is Animal Size so Important? Cambridge University Press, New York.
- Sillero, N., 2011. What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. Ecol. Model. 222, 1343–1346.
- Somme, L., 1995. Invertebrates in Hot and Cold Arid Environments. Springer-Verlag, Berlin.
- Valladares Faúndez, P., Álvarez Henríquez, N., Urrutia Osorio, N., Olivares Zuleta, F., Alvarado Orellana, S., 2015. Dieta del aguilucho común *Geranoaetus polyosoma* (Quoy & Gaimard 1824) en la Región de Atacama, Chile. Gayana 79, 121–127.
- Vidal, M.A., Pizarro-Araya, J., Jerez, V., Ortiz, J.C., 2011. Daily activity and thermoregulation in the predator – prey interaction during Flowering desert in Chile. J. Arid Environ. 75, 802–808.
- Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press-Elsevier, London.
- Zachariassen, K.E., Andersen, J., Maloij, G.M.O., Kamau, J.M.Z., 1987. Respiratory water loss and metabolism of beetles from arid areas in East Africa. Comp. Biochem. Physiol. A 86, 403–408.
- Žagar, A., Carretero, M.A., Marguč, D., Simčič, T., Vrezec, A., 2017. A metabolic syndrome in terrestrial ectotherms with opposite elevation and distribution patterns. Ecography (in press).
- Zar, J.H., 1984. Biostatistical Analysis, second ed. Prentice-Hall, Inc., Englewood Cliffs.